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# Tasmanian devil (Sarcophilus harrisii) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification

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# Tasmanian devil (*Sarcophilus harrisii*) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification

OLIVER J. F. BROWN

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Based on a review here, the most recent Tasmanian devil remains on the mainland date from between 3000 and 4000 years BP in three isolated populations. A widely promulgated recent date within the last 500 years is rejected. Previous studies have found the arrival of the dingo (>3500 BP) to be the only suitable coincident extinction cause, although Aboriginal cultural changes have also been recently implicated. I propose that increased climate variability associated with the onset of the El Niño Southern Oscillation after 6000 BP and a subsequent intensification *ca* 3000 BP was also a causative factor. Other causes are not rejected, but rather all are placed within a multicausal model. Tasmanian devils are particularly susceptible to climate variability because they are the only specialised scavenger in Australia. Specialised scavengers are mostly limited by variability in the availability of carrion, and this would have increased significantly with ENSO. The fossil record (and persistence in Tasmania) indicates a range contraction of Tasmanian devils from the late Pleistocene onwards towards isolated refugia into those parts of the country least affected by ENSO related climate variability.

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Key words**:** Tasmanian devil, El Niño, Holocene, extinction, multicausality.

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IT HAS widely been proposed that the Australian mainland extinction of the Tasmanian Devil (*Sarcophilus harrisii*) occurred as a result of the introduction of the dingo (*Canis lupus dingo*) some time before 3500 years ago (Gollan 1984, Corbett 1995). More recently, Johnson & Wroe (2003) suggested that human impact associated with Holocene intensification of Aboriginal settlement and resource use might also have had a role in the devil's mainland demise. In doing so, they did not reject dingoes as a contributive cause, but rather presented human impact as an alternative explanation, offering that a multicausal model may in fact be appropriate. This paper aims to extend the range of likely multicausal factors to include the mid-Holocene onset and subsequent intensification of the El Niño Southern Oscillation (ENSO).

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It is proposed that climate variability has been underestimated in previous attempts to assess the effects of climate change on Holocene extinctions in Australia in general, and more specifically on the ecology of scavengers. The idea that ENSO onset affected devils in particular relies on the fact that Tasmanian devils, as specialised scavengers, are unavoidably constrained by the temporally and spatially variable availability of carrion, and that ENSO onset would have significantly increased that variability. That is, rather than having to be able to cope with lean seasons, or occasional lean years, the lean periods of an ENSO-affected environment would have covered entire multi-year El Niño or La Niña events. This 'ENSO hypothesis' shares similarities with explanations involving the effects of dingoes and Aboriginal intensification in that ENSO onset: 1) preceded

the final mainland extinction of devils; 2) had a different effect on most of mainland Australia than on Tasmania; and 3) would have had a negative effect on devils that is clearly explicable. Although somewhat limited by sample size, this hypothesis is well supported by the fossil record.

## The Tasmanian devil in mainland Australia

The Tasmanian devil is currently the world's largest carnivorous marsupial, since the loss of the thylacine (*Thylacinus cyanocephalus*) from Tasmania during the twentieth century. Devils now only occur in parts of Tasmania, but were once also widespread in mainland Australia, with Pleistocene fossil records occurring in all but the most arid and inland parts of the continent (typically referred to *S. laniarius*) (Dawson 1982). Interpretation of the fossil record for Tasmanian devils is somewhat problematic due to a limited sample size and issues with dating, particularly regarding the extinction period. However, the current evidence suggests a range contraction of mainland devils from a circumcontinental distribution at some stage(s) of the Pleistocene to three relict populations by the Holocene. These populations were:

- Northern. Based on a single fossil in the top of the Northern Territory near Darwin dated to 3120±100 (Calaby & White 1967). There is also reported evidence of devils in this region based on rock art (Flood 1995, pp. 390).

- South-western. Holocene devils have been reported by a number of authors from sites in southwest Western Australia (Butler & Merrilees 1971, Lundelius 1960, Archer & Baynes 1972). Despite the problems with the reliability of some dates (discussed below), generalised dating to the mid-late Holocene and after sea-level stabilisation can be supported.

- South-eastern. Holocene devils have been reported from a number of locations from the Murray River mouth to Port Philip Bay, the most recent of which is from Fromms Landing, dated at 3240±80 (Mulvaney 1960, Gill 1971, Dawson 1982). Some early-mid Holocene records also exist for parts of the middle reaches of the Murray River well into the semi-arid zone – most notably those evidenced by devil tooth necklaces found in some Aboriginal burials, one made from the teeth of at least forty-seven individual devils (Macintosh 1971, Pardoe 1995). This population also extended further into NSW and up into Queensland at the end of the Pleistocene (Dawson 1982) and would have been cut off from the Tasmanian population with the flooding of the Bass Strait land bridge at the start of the Holocene.

More recent dates for mainland Tasmanian devil remains have also been claimed. However, method-ological issues surround the dating such that all either have been, or should be, rejected; particularly a very commonly referenced date of 430 ± 160 BP reported by Archer & Baynes (1972). This date has been widely used, including standard texts on Australian archaeology, influential popular natural history books, and many significant peer-reviewed papers (e.g. Bradshaw & Brook 2005, Dodson *et al.* 1992, p. 132; Glen & Dickman 2005, Flannery 1994, pp. 384; Flood 1995, pp. 181; Mulvaney & Kamminga 1999, pp. 124; Low 2001, pp. 12; Johnson & Wroe 2003, Jones *et al.* 2004). In the detail of the paper, the authors clearly explain that the devil tooth in question was not recovered from the dated deposit and that they themselves were not certain of its provenance (Archer & Baynes 1972, pp. 82). It was instead "collected from the foot of the cliff immediately below a small opening that leads back into the solution cavity in Cave 1 that contained the Cave 1 deposit. Bone material in the solution cavity was found scattered as far as

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this opening in the cliff face. There were other small bones lying with the *S. harrisii* tooth that resembled the material from the Cave 1 deposit. This suggests that a quantity of material including the Sarcophilus tooth fell from the deposit" (Archer & Baynes 1972, pp. 82). This is a possible scenario, no doubt, but certainly not rigorous enough to date the continental extinction of a species. In addition to the issue of provenance, only one date was obtained, and was based on a single sample taken from "throughout the 8cm interval excavated" (Archer & Baynes 1972, pp. 86) – this just provides an age for something in the deposit, not the entire deposit and all that may have been in it, and certainly says nothing conclusive about its antiquity. Archer & Baynes (1972, pp. 87) also suggest another devil specimen from a deposit dated to 620 ± 90 BP but omit any statement of methodology or details on the actual association between the dating and the specimen, and so this date cannot be accepted, let alone rejected. Another late date for continental devil remains of 538 ± 200 BP in western Victoria given by Gill (1951 1953 1955) has subsequently been amended to *ca* 5000 BP by Gill himself (1971),

## The timing of ENSO onset and mainland devil extinction

The effects of climate on the mainland extinction of the Tasmanian devil have previously been discounted on the basis of the perception of climate stability through the Holocene. Johnson & Wroe for example largely discount the effects of climate (2003, pp. 1009), although offer a concluding caveat that "it is at least possible that a reduction in rainfall exacerbated the impact on native vertebrates of intensification and arrival of the dingo" (2003, pp. 1013). Current understanding of the ecological effects of ENSO and its palaeoclimatic history, provides two important revisions: 1) The critical effects of ENSO are not so much about 'reduction in rainfall' and climatic averages as they about rainfall variability and the intensity and duration of severe climatic events such as drought; and 2) The timing of ENSO-related changes are very significant with regard to mainland devil decline. Based on a wide array of environmental data a consensus of opinion now supports an onset of ENSO after 6000 BP (e.g. Loubere *et al.* 2003, Sandweiss *et al.* 1996). Moreover, it is believed that the magnitude of ENSO experienced an abrupt increase at about 3000 BP (Gagan *et al.* 2004).

These ENSO-related climatic changes are clearly coincident with the process of devil extinction suggested by the fossil record. The late Pleistocene record is suggestive of a general range contraction away from inland Australia that is coincident with a general increase in climate variability from about 45000 BP (Kershaw *et al.* 2003). From the start of the Holocene until ENSO onset after 6000 BP there is the suggestion of a further contraction to the three isolated near-coastal areas described above. The apparent disappearance from semi-arid inland Murray River sites is co-incident with climate-related environmental changes associated with ENSO onset in that area (Cupper *et al.* 2000). The final mainland extinction coincides with the abrupt increase in ENSO intensity at around 3000 BP (Gagan *et al.* 2004). All three final refugia occur in parts of the country that are the least affected by climate variability. The northern population area, while still affected by ENSO, experiences considerable amelioration from overall climate variability because of the relative reliability of the monsoon at that latitude and position in relation to the coast. The south-western and the southern population areas are those parts of the country least affected by ENSO itself (Allan *et al.* 1996, Dai & Wigley 2000). This is also true of Tasmania.

## The effects of ENSO and the ecology of scavenging

In addition to developments in our understanding of the antiquity of ENSO, there has also been a growing recognition of the ways in which ENSO shapes many ecosystems (e.g. Holmgren *et al.* 2001, Stenseth *et al.* 2002, Letnic

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& Dickman 2005). This is true across most of Australia, particularly in the north, east and centre of the continent (Allan *et al.* 1996, Dai & Wigley 2000). In particular, the climatic variability associated with ENSO creates subsequent variability in the abundance of certain key limiting resources that are related to rainfall. This has been most clearly recognised in the boom and bust population patterns that occur sequentially in plant, herbivore and carnivore productivity or abundance (e.g., Jaksic *et al.* 1997, Letnic *et al.* 2005). In addition to such bottom-up trophic biomass variability that can be linked to ENSO, variability in top-down mortality effects are also linked to ENSO (Brown & Ernest 2002). Associations between El Niño-related drought and mass deaths of kangaroos and domestic stock are well established (e.g. Robertson 1986). It follows that one of the effects of ENSO is to create variability in the availability of carrion, and consequently the ecology of scavenging (Brown *et al*. 2006).

For most carnivores, variation in the availability of live prey and carrion that occur in relation to ENSO phases leads to changing propensities for hunting and scavenging among facultative scavengers. For example, during periods of live prey scarcity, scavenging increases in importance among species that are more typically seen as predatory. Such dietary shifts have been described according to the term 'environmentally modulated predation' (Newsome *et al.* 1989) and have been studied in the diets of all major facultative scavengers in Australia (e.g. Brooker & Ridpath 1980, Catling 1988, Paltridge 2002, Guarino 2001). With the possible exception of lace monitors (*Varanus varius*) (Guarino 2001), the most significant limiting resource affected by ENSO for all these species is live prey, and not carrion.

For an obligate (or full-time) scavenger, carrion is the most significant limiting resource, and it can be typified as being temporally and spatially highly variable in its availability. For example, it has been proposed that the reason that vultures are the only obligate scavengers in the world is because only a large soaring flier can deal with the unpredictability of carrion (Ruxton & Houston 2004). This is because they can travel with great energy efficiency and have a body size capable of accommodating significant food reserves. Specialised scavengers, as defined here, are those facultative scavengers for which carrion is a greater limiting resource than live prey. Among Australian terrestrial vertebrates it is also proposed here that the Tasmanian devil is the only specialised scavenger, and indeed that it is one of the few specialised mammalian scavengers in the world. This is not to challenge the observation that devils are capable of hunting relatively large game on occasion (e.g. Owen & Pemberton 2005), but simply to defer to the typical observation that scavenging presents their more common or successful foraging strategy.

The Tasmanian devil has some remarkable adaptations to support its role as a specialised scavenger. The gait of the devil has been described as an easy, loping 'rocking-horse gait' that is similar to that of the hyena for reasons of convergence. That is, they have an energy efficient gait that allows them to cover large distances in search of spatially unpredictable carrion, (Guiler 1970a, Guiler 1992). Tasmanian devils have low basal metabolic rates (BMR) – even among marsupials, which have BMRs typically <70% that of their eutherian counterparts (Nicol & Maskrey 1980, Hume 1999, Hume 2003). Devils are able to further extend the metabolic efficiency of a low BMR through: Being capable of undergoing shallow daily torpor; having a high passive variation in labile body temperature (31-38º); and spending a large proportion of time in paradoxial sleep which can be accompanied by a further relaxation in thermoregulation (Nicol 1982, Jones *et al*. 1997, Hume 1999). These efficiencies can be seen to help the devil cope with the periods of food scarcity that come with the temporal unpredictability of carrion. Devils are also able to make the most of food when they find it by being able to consume up to 40% of their body weight at a sitting and can consume all parts of the carcass – including the teeth (Pemberton &

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Renouf 1993, Guiler 1970b). Their competency as osteophages has been frequently observed and is supported by them having the highest bite force (scaled to size) of any extant species of mammal as well as highly robust teeth and skulls (Wroe *et al.* 2005).

Such features make the Tasmanian devil better adapted to scavenging than any other Australian mammal. While female and young devils have been found to consume a greater amount of live and arboreal prey than the dimorphically larger adult males, the species as a whole is dependant enough upon scavenging to suppose that carrion is likely to be a more significant limiting resource than live prey (Jones & Barmuta 1998). Consequently, their abundance and distribution would be significantly affected by any serious exacerbation in the temporal and spatial unpredictability of carrion. Such a change will have occurred in mainland Australia with the mid-Holocene onset and intensification of ENSO.

As specialised scavengers affected by carrion variability, Tasmanian devils would be affected not only by the occurrence or frequency of ENSO events, but by their duration. ENSO variability as we currently experience it includes pluvial and drought periods that can last for several years. This means that the effect of ENSO on patterns of carrion availability is not just towards greater unpredictability but also longer duration of both scarcity and abundance. With regard to Tasmanian devils, we can postulate that such oscillations at a multi-year timescale could have a very serious effect on breeding ecology. "Devils are relatively short-lived animals (< six years), do not breed until two years of age, become senescent after around four years old and can only rear one litter a year" (DPIWE 2005a). A multi-year event could therefore extend across the duration of the entire breeding life of a single generation. Theoretically at least, periods of carrion scarcity would not even have to result in starvation mortality, as simply poor breeding success would be enough to devastate a population during a three year event. The potential suggested by Owen & Pemberton (2005, pp. 66) of a devil population with adequate resources doubling in a single year may only provide for population resilience over short time spans and wide geographic spread – the isolation of populations and multi-year periods of reproductive suppression proposed here would still be failed by this potential fecundity. The semalparousness in response to population decline observed in the recent decimations by facial tumour disease (i.e., breeding activity and subsequent death of younger males following the mortality of normally dominant older males, also indicates a short-term resilience that would not be suited to long-term ENSO-related stress.

## Discussion

Above and beyond any evidence that can be advanced for the causes of extinctions that is observed through the fractured light of the fossil record, far clearer evidence from recent historical extinctions suggests that single causes are almost never responsible (Didham *et al*. 2005, Glen & Dickman 2005, Wroe 2005). Monocausal extinctions have only ever been observed on islands and are always rapid (e.g., Vázquez-Domínguez *et al*. 2004). The extinction of Tasmanian devils on mainland Australia occurred at the end of a long-term range contraction over many millennia. Were the impact of dingoes to be a single cause, then it had to have taken around a thousand years or more to take effect – and also to have acted independently of the other changes going on at the time. Not only were ENSO onset and Aboriginal intensification coincident with devil decline, but also changing sea levels, the loss of the previously sympatric and co-evolved thylacine, and the arrival of whatever diseases accompanied dingoes.

The causes involved in extinction are frequently the proximal manifestations of a number of more distal causes, so that even apparently single causes can be part of deeper multicausal processes. Aboriginal intensification for example, can be contextualised as a possible response to changing environmental variables – of which climate and ENSO onset are the most likely (Rowland 1999). The effects of dingoes

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had to have been similarly complex. Among the changes in the ecology of scavenging resulting from ENSO-related variability in carrion abundance would have been a greater success of facultative scavengers such as dingos. Consequently, even direct replacement of devils by dingoes, or 'superior adaptability' as Corbett (1995) described it, occurred within a multicausal context including climate. Furthermore, the arrival of the dingo was almost certainly a human-mediated event related to the movements of Asian seafarers to the north of Australia. Their movements would have been dependant on both the terrestrial and marine ecology of what is now the Indonesian archipelago and monsoon patterns – all of which change in relation to ENSO (Lau *et al*. 2000, Kinter *et al*. 2002).

Were the onset of ENSO to have occurred in the mid-Holocene without Aboriginal intensification or the arrival of the dingo, it is possible that the Tasmanian devil would not have become extinct on mainland Australia – at least until European invasion and the start of the processes leading to the demise of other fauna such as quolls (*Dasyurus* spp.). However, in the absence of factors other than dingoes, it is possible that they alone would not have lead to the mainland extinction of the Tasmanian devil either – feral dogs have certainly not been the devils greatest threat in Tasmania over the last 150 years. Such speculation may not be appropriate in this case anyway, because of the ways in which all three of the factors so far implicated in mainland devil extinction are inseparable. Some causes are more direct or immediately apparent than others ('proximal' as I have described them here), but deeper underlying ('distal') factors are no less causative. ENSO, in its effects on the mainland extinction of devils, has both proximal and distal aspects.

Much of the palaeoecological history of Australia in relation to ENSO remains to be uncovered. For example, the Holocene mainland extinction of the Tasmanian native-hen (*Gallinula mortierii*), a flightless wetland rail, might similarly have involved ENSO. In this case the effect of ENSO would have related to the increasing ephemerality of mainland wetlands and the impact that this would have had on birds unable to fly to and from increasingly variable resources (see Roshier *et al*. 2001). Previous explanations have been similar to those offered for mainland devils, leaning mostly towards the effects of dingoes and people for the final phase of extinction (Baird 1991, Johnson & Wroe 2003). On a deeper timescale, Pleistocene extinctions are also increasingly open to review that considers variability as a more important factor in climate change (e.g. Kershaw *et al*. 2003). Increasingly also, multicausal hypotheses in which climate is more than just a backdrop against which other extinction processes took place are in the ascendancy (Wroe 2005). It is logically implausible that the complexity of ecology and the multicausal processes of extinction as we find them today are not in some way mirrored in the past.

Understanding the mainland extinction of the Tasmanian devil in all its complexity is potentially more important now than ever. The remaining extant population of devils, until recently safe in their island home despite the many changes of the historical period, now face the possibility of full extinction. They are under pressure from the vandalistic introduction of the red fox (*Vulpes vulpes*) from the mainland whilst at the same time being decimated by 'devil facial tumour disease' (Bradshaw & Brook 2005, DPIWE 2005a, Pemberton & Owen 2005). Populations in some areas have been reduced by over 90% and there is no known cure for the disease. The Tasmanian devil has now been listed as a vulnerable species under Tasmanian legislation, and captive insurance populations have been isolated in preparation for the worst-case scenario of extinction in the wild (Bostanci 2005, DPIWE 2005a-b, Pemberton & Owen 2005). At whatever stage the current decline can be halted, more than one cause will need to be addressed. The next stage will be akin to effecting an extinction in reverse. This will be necessarily complex, and probably frustratingly experimental (like most reintroductions); so the more factors that can be accounted for the better.

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## References

Allan, R. J., Lindesay, J. & Parker, D., 1996. *The El Niño southern oscillation & climatic variability*. CSIRO Publishing, Collingwood, Vic. 416 pp.

Archer, M. & Baynes, A., 1972. Prehistoric mammal faunas from two small caves in the extreme south-west of Western Australia. *Journal of the Royal Society of Western Australia 55*, 80-89.

Baird, R.F., 1991. The dingo as a possible factor in the disappearance of *Gallinula mortierii* from the Australian mainland. *The Emu 91,* 121-122.

Bostanci, A., 2005. A devil of a disease. *Science 307,* 1035.

Bradshaw, C.J.A. & Brook, B.W., 2005. Disease and the devil: density-dependent epidemiological processes explain historical population fluctuations in the Tasmanian devil. *Ecography 28*, 181-190.

Brooker, M.G. & Ridpath, M.G., 1980. The diet of the wedge-tailed eagle, *Aquila audax*, in Western Australia. *Australian Wildlife Research 7*, 433-452.

Brown, J.H. & Ernest S.K.M., 2002. Rain and Rodents: Complex Dynamics of Desert Consumers. *BioScience 52*, 979-987.

Brown, O.J.F., Field, J. & Letnic, M., 2006. Variation in the taphonomic effect of scavengers in semi-arid Australia linked to rainfall and the El Niño Southern Oscillation (ENSO). *International Journal of Osteoarchaeology 16*, 165-176.

Butler, W.H. & Merrilees, D., 1971. Remains of *Potorous platyopus* (Marsupilia: Macropodidae) and other mammals from Bremer Bay, Western Australia. *Journal of the Royal Society of Western Australia 54*, 53-58.

Calaby, J.H. & White, C., 1967. The Tasmanian devil (*Sarcophilus harrisii*) in northern Australia in recent times. *Australian Journal of Science 29*, 473-475.

Catling, P.C., 1988. Similarities and contrasts in the diets of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Australian Wildlife Research 15*, 307-317.

Corbett, L., 1995. *The dingo in Australia and Asia*. University of New South Wales Press, Sydney. 200 pp.

Cupper, M.L., Drinnan, A.N. & Thomas, I., 2000. Holocene palaeoenvironments of salt lakes in the Darling Anabranch region, south-western New South Wales, Australia. *Journal of Biogeography 27,* 1079-1094.

Dai, A. & Wigley, T.M.L., 2000. Global patterns of ENSO-induced precipitation. *Geophysical Research Letters 27*, 1283-1286.

Dawson, L. 1982. Taxonomic status of fossil devils (*Sarcophilus*, Dasuryidae, Marsupialia) from late Quaternary eastern Australian localities. In *Carnivorous Marsupials*, M. Archer ed., Royal Zoological Society of New South Wales, Sydney, 517-525.

Didham, R.K., Ewers, R.M., & Gemmell, N.J., 2005. Comment on "Avian extinction and mammalian introductions on oceanic islands". *Science 307*, 1412.

Dodson, J., Fullagar, R. & Head, L., 1992. Dynamics of environment and people in the forested crescents of temperate Australia. In *The Naïve Lands: Prehistory and environmental change in Australia and the southwest Pacific*, J Dodson ed., Longman & Cheshire, Melbourne, 115-159.

DPIWE, 2005a. *Devil facial tumour disease (DFTD): disease management strategy*. Department of Primary Industries, Water and Environment (Tasmania). <http://www.dpiwe.tas.gov.au/inter.nsf/Attachments/LBUN-6996MH/$FILE/DFTD_DMS_Feb05a.pdf>, accessed Aug 05 2005.

DPIWE, 2005b. *Devil facial tumour disease update, April 2005*. Department of Primary Industries, Water and Environment (Tasmania). <http://www.dpiwe.tas.gov.au/inter.nsf/Attachments/LBUN-6B97AA/$FILE/dftd%20update%20April%202005.pdf>.

Flannery, T., 1994. *The Future Eaters*. Reed Books, Sydney. 432 pp.

Flood, J.,1995. *Archaeology of the Dreamtime*. Angus & Robertson, Sydney. 320 pp.

Gagan, M.K., Hendy, E.J., Haberle, S.G. & Hantoro, W.S., 2004. Post-glacial evolution of the Indo-Pacific Warm Pool and El Nino-Southern Oscillation. *Quaternary International 118-19*, 127-143.

Gollan, K., 1984. The Australian dingo: in the shadow of man. In *Vertebrate zoogeography and evolution in Australia*, M. Archer & G. Clayton eds., Hesperian Press, Perth, 921-927.

Gill, E.D., 1951. Aboriginal kitchen middens and emerged shell beds. *Mankind 4*, 249-254.

Gill, E.D., 1953. Distribution of the Tasmanian devil, the Tasmanian wolf and the dingo in S.E. Australia in Quaternary time. *Victorian Naturalist 70*, 86-90.

Gill, E.D., 1955. Aboriginal midden sites in western Victoria dated by radiocarbon analysis. *Mankind 5*, 51-5.

Gill, E.D., 1971. The Australian Aborigines and the Tasmanian Devil. *Mankind 8*, 59-63.

Glen, A.S. & Dickman, C.R., 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews 80,* 1-15.

Gollan, K., 1984. The Australian dingo: in the shadow of man. In *Vertebrate zoogeography and evolution in Australia*, M. Archer & G. Clayton eds., Hesperian Press, Perth, 921-27.

Guarino, F., 2001. Diet of a large carnivorous lizard,

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*Varanus varius*. *Wildlife Research 28*, 627-630.

Guiler, E.R., 1970a. Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). I Numbers, home range, movements, and food in two populations. *Australian Journal of Zoology 18*, 49-62.

Guiler, E.R., 1970b. Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). II Reproduction, breeding, and growth of pouch young. *Australian Journal of Zoology 18*, 63-70.

Guiler, E.R., 1992. *The Tasmanian devil*. St David's Park Publishing, Hobart. 20 pp.

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J.R. & Mohren, G.M.J., 2001. El Nino effects on the dynamics of terrestrial ecosystems. *Trends In Ecology & Evolution 16*, 89-94.

Hume, I.D., 1999. *Marsupial nutrition*. Cambridge University Press, Cambridge. 434 pp.

Hume, I.D., 2003. Nutrition of carnivorous marsupials. In *Predators with pouches: the biology of carnivorous marsupials*, M.E. Jones, C.R. Dickman & M. Archer eds, CSIRO Publishing, Collingwood 221-228.

Jaksic, F.M., Silva, S.I., Meserve, P.L., & Gutierrez, J.R., 1997. A long-term study of vertebrate predator responses to an El Nino (ENSO) disturbance in western South America. *Oikos 78*, 341-354.

Johnson, C.N & Wroe, S., 2003. Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact? *The Holocene 13*, 1009-1016.

Jones, M.E. & Barmuta, L.A., 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. *Journal of Animal Ecology 67*, 410-421.

Jones, M.E., Paetkau, D., Geffen, E. & Moritz, C., 2004. Genetic diversity and population structure of Tasmanian devils, the largest marsupial carnivore. *Molecular Ecology 13*, 2197-2209.

Jones, M.E., Grigg, G.C., & Beard, L.A., 1997. Body temperatures and activity patterns of Tasmanian devils (*Sarcophilus harrisii*) and eastern quolls (*Dasyurus viverrinus*) through a subalpine winter. *Physiological Zoology 70*, 53-60.

Kershaw, P., Moss, P. & Van der Kaars, S., 2003. Causes and consequences of long-term climatic variability on the Australian continent. *Freshwater Biology 48*, 1274-1283.

Kinter III, J.L., Miyakoda, K., & Yang, S., 2002. Recent change in the connection from the Asian Monsoon to ENSO. *Journal of Climate 15*, 1203-1215.

Letnic, M., Tamayo, B. & Dickman, C.R., 2005. The responses of mammals to La Niña (ENSO)-associated rainfall, predation and wildfire in the Simpson Desert, Australia. *Journal of Mammalogy 86*, 689-703.

Letnic, M. & Dickman, C.R., In press. Boom means bust: interactions between the El Niño / Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation*.

Lau, N. & Nath, M., 2000. Impact of ENSO on the variability of the Asian-Australian Monsoons as simulated in GCM experiments. *Journal of Climate 13*, 4287-4309.

Loubere, P., Richaud, M., Liu, Z. & Mekik, F., 2003. Oceanic conditions in the eastern equatorial Pacific during the onset of ENSO in the Holocene. *Quaternary Research 60*, 142-148.

Low, T., 2001. *Feral Future: The untold story of Australia's exotic invaders*. Penguin, Camberwell.

Lundelius, E.L., 1963. Vertebrate remains from the Nullabor caves. *Journal of the Royal Society of Western Australia 46*, 75-80.

Macintosh, N.W.G., 1971. Analysis of an Aboriginal skeleton and a pierced tooth necklace from Lake Nitchie, Australia. *Anthropologie 9*, 49-62.

Mulvaney, D.J., 1960. Archaeological excavations at Fromm's Landing on the lower Murray River, South Australia. *Proceedings of the Royal Society of Victoria 73*, 53-85.

Mulvaney, J. & Kamminga, J., 1999. *Prehistory of Australia*. Allen & Unwin, Sydney. 480 pp.

Newsome, A.E., Parer, I. & Catling, P.C., 1989. Prolonged prey suppression by carnivores: predator-removal experiments. *Oecologia 78*, 458-467.

Nicol, S.C., 1982. Physiology of the Tasmanian devil. In *Carnivorous marsupials*, vol. 1, M. Archer ed, Royal Zoological Society of New South Wales, Sydney, 273-278.

Nicol, S.C. & Maskrey, M., 1980. Thermoregulation, Respiration And Sleep In The Tasmanian Devil, *Sarcophilus harrisii* (Marsupialia, Dasyuridae). *Journal Of Comparative Physiology 140*, 241-248.

Owen, D & Pemberton, D., 2005. *Tasmanian Devil: A Unique and Threatened Animal*. Allen & Unwin, Sydney. 225 pp.

Paltridge, R., 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research 29*, 389-403.

Pardoe, C., 1995. Riverine, biological and cultural evolution in southeastern Australia. *Antiquity 69*, 696-713.

Pemberton, D. & Renouf, D., 1993. A field-study of communication and social-behavior of the Tasmanian Devil at feeding sites. *Australian Journal of Zoology 41*, 507-526.

Robertson, G., 1986. The mortality of kangaroos in drought. *Australian Wildlife Research 13*, 349-154.

Roshier, D.A., Whetton, P.H., Allan R.J. & Robertson, A.I., 2001. Distribution and persistence of temporary wetland habitats in arid Australia in relation to climate. *Austral Ecology 26*, 371-384.

Rowland, M.J., 1999. Holocene environmental variability: have its impacts been underestimated in Australian pre-history? *The Artefact 22*, 11-48.

Ruxton, G.D., & Houston D.C., 2004. Obligate vertebrate scavengers must be large soaring fliers. *Journal Of Theoretical Biology 228*, 431-436.

Sandweiss, D.H., Maasch, K.A., Burger, R.L., Richardson

III, J.B. Rollins, H. B. & Clement, A., 1996. Variation in El Niño frequencies: climate records and cultural consequences in ancient Peru. *Geology 29*, 603-606.

Stenseth, N.C., Mysterud, A., Ottersenl, G., Hurrell, J.W, Chan, K.S. & Lima, M., 2002. Ecological effects of climate fluctuations. *Science 297,* 1292-1296.

Vázquez-Domínguez, E., Ceballos, G., & Cruzado, J., 2004. Extirpation of an insular subspecies by a single introduced cat: the case of the endemic deer mouse *Peromyscus guardia* on Estanque Island, Mexico. *Oryx 38*, 347-350.

Wroe, S., 2005. On little lizards and the big extinction game. *Quaternary Australasia 23*, 8-11.

Wroe, S., McHenry, C., & Thomason, J., 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society of London, Series B - Biological Sciences 272*, 619-625.

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